Feeding Strategies of Five Nocturnal Prosimians in the Dry Forest of the West Coast of Madagascar

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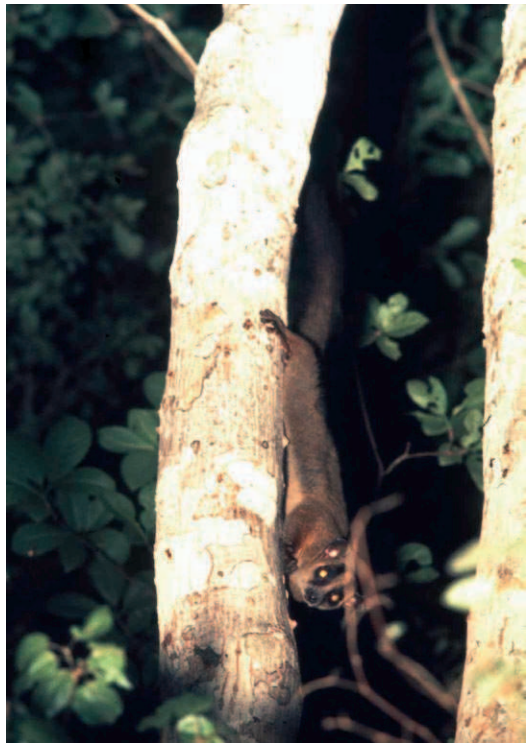

Microcebus **and** ***Phaner*** **foraging at night in the Marosalaza forest, in 1974 (photos C.M. Hladik)**

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2 *Feeding Strategies of Five Nocturnal Prosimians in the Dry Forest of the West Coast of Madagascar*

C. M. HLADIK, P. CHARLES-DOMINIQUE, and J. J. PETTER

INTRODUCTION

The adaptive strategy of animal populations allows a species increased fitness in response to important variations of environmental conditions mainly affecting food availability. In evolutionary terms, some species invest in the efficiency of reproductive functions for maximum population growth when conditions permit (r strategy), while other species maintain a fairly constant population (K strategy) through maximum investment in individual fitness (MacArthur and Wilson, 1967). The predictability of food production is a determinant parameter of such mechanisms, the K strategy existing only in the presence of regular cycles of overall food production. By contrast, species adaptation to food resources described as "generalization" and "specialization" (MacArthur, 1965) may or may not correspond to the temporal patterning of food availability. For instance, specialized species such as most folivorous mammals are adapted to a set of predictable food resources (A. Hladik, 1978), while other specialists, mainly among monophagous invertebrates, evolved towards r strategies to maximize the output from locally abundant resources unevenly distributed in space and time (Wilson, 1975).

Among primates, feeding strategies which have been observed in different species are intermediate cases of specialization concerning differential utilization of food resources. The most specialized is a "low-cost and low-energy return" strategy of some folivores (Hladik,1977a) which allows large populations to subsist on the most abundant but least nutritious plants. The most generalized is the "high-cost and high-energy return" strategy of many Cercopithecinae and Chimpanzees (Hladik, 1977b). Both

tendencies are obviously the expression of the K strategy, and tend to maintain constant population densities (Charles-Dominique and Hladik, 1971). Although primate population ecology suffers from the small size of most samples observed, the accuracy of a multitude of field studies has allowed detailed analysis of feeding strategies in relation to physiology, behavior, and sociology, which support these views (C. M. Hladik and Chivers, 1978).

A comparison of the different adaptations of the nocturnal prosimian species of the Marosalaza forest (West Coast of Madagascar) provides additional information of this kind. In this region, the environment presents a highly variable cycle (Chapter 1), with predictability of food supply only possible on a long-term basis. The prosimian species have adopted several ecophysiological or behavioral solutions, a brief account of which has already been presented by Petter (1978). Two of these species, *Phaner furcifer* and *Microcebus coquereli,* are the main subject of other chapters included in this volume, by Charles-Dominique and Petter, and by Pages, respectively. A third species, *Lepilemur ruficaudatus,* can be compared to other Sportive Lemurs studied in detail elsewhere (C. M. Hladik and Charles-Dominique, 1974). Accordingly, in the present comparative study, we mainly develop detailed information concerning the two Cheirogaleinae, *Cheirogaleus medius* and *Microcebus murinus,* which live in sympatry with the three other nocturnal species in the Marosalaza forest.

This chapter is based on data obtained during successive and partly overlapping field studies of the authors (J. J. Petter, October/November, 1973 and January/February, 1974; C. M. Hladik, December, 1973/January, 1974; P. Charles-Dominique, November/December, 1973 and May/June, 1974 and is completed by field observations of other participants of the Morondava Programme (G. F. Pariente and E. Pages). The interpretation of most results was permitted by careful analysis of physiological cycles of the different prosimians, conducted simultaneously and following completion of the field work, in the animal house of the Brunoy Laboratory (see Chapters 2, 6, and 7).

The different techniques for recording data on plant production and for animal trapping and marking, which are also common to other papers in this volume, will be briefly described in the relevant sections.

SEASONAL VARIATIONS IN FOOD PRODUCTION AND FOOD COMPOSITION IN THE MAROSALAZA FOREST

The environmental conditions in the Marosalaza forest are described in Chapter 1. Plant diversity is not as important as in most tropical forests in-

habited by primates. Nevertheless, different life cycles of tree and liana species provide a successional emergence of various food resources.

Yearly variations, in terms of the number of plant species bearing flowers, fruit, and new leaves (Fig. 1), provide only an approximate picture of the actual changes of food availability in the Marosalaza forest, since the biomass of the different species varies considerably. Accordingly, an index was calculated which takes into account the total basal area of the most common species present in the sample and reflects the total biomass. The values obtained by adding these "biomass indices" yielded overall variations roughly correlated with species abundance: a peak for flowers in November, but a slightly more even distribution of fruit production between December and June. Since these different values are not significant for plant species present in small quantity, potential food availability could not be recorded in terms of absolute production, except during a limited period (see Table V, Chapter 1). Nevertheless, the different methods of approach yielded sufficiently similar results in terms of relative variation of potential food production to consider Fig 1. as a valid base for comparing the adaptations of different prosimian species.

Seasonal Variations in Flowers

There is a very marked period of flowering in October/November preceding the rainy season, which lasts for only a short time after the rain

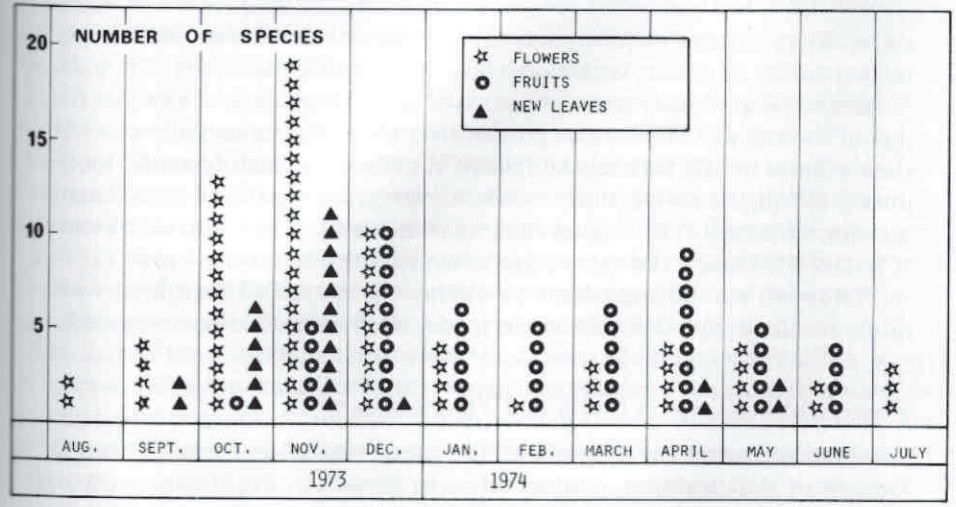

Fig. 1. Variation of food availability throughout the year, in the Marosalaza forest, according to the number of species producing potential foods in a sample of 2200 m² (J.- P. Abraham's transect analyzed by A. Hladik, Chapter 1, Table I).

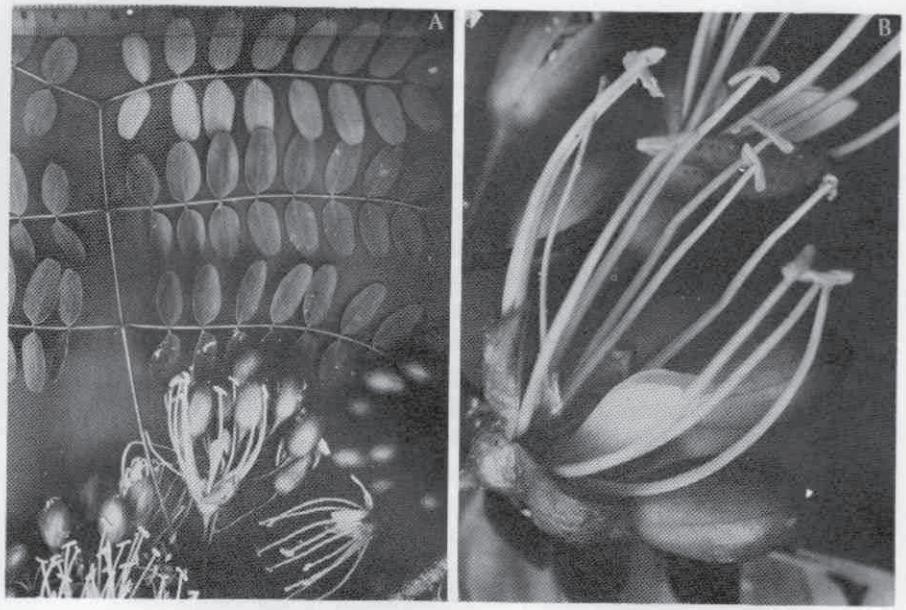

Fig. 2. The Boy flower, *Delonix floribunda* (A), in which was found the most abundant production of nectar. The detail (B) shows the unique central petal totally filled with 0.5 gm of nectar (species 38 in Appendix I of Chapter 1; photos by C. M. Hladik).

starts. Many species of Marosalaza forest plants bear flowers with a very large quantity of nectar, such as the Boy, *Delonix floribunda* (28) * (Fig.2). Sussman (1978) already noted the importance of some large flowers in the diet of diurnal and crepuscular prosimians, which are major pollinators of these plants. In Marosalaza, the sudden abundance of such potential foods during the austral spring, corresponds to changes in physiological cycles of activity, especially in *Microcebus murinus* and *Cheirogaleus medius* (Chapter 6). During the dry season, only a limited number of plants produce flowers, but the large Baobabs, *Adansonia* spp. (20/21) might provide an important supply for still active species such as *Microcebus coquereli.*

Seasonal Variations in Fruits and Young Leaves

Fruits are available throughout the rainy season and until June. In December, the maximum production of fruits such as the Malagasy plum, *Flacourtia indica* (83), the fruit of Iron wood, *Strychnos decussata* (93), the Forest grape, *Cyphostemma pachypus* (180), a bottle-like vine, (see Tables

* The numbers in parentheses refer to Appendix I of Chapter 1.

I and II, Chapter1), occurs simultaneously with the decreased availability of nectar and other edible parts of flowers produced by different species. Fruits are also abundant in February/March, when the young of different prosimian species start feeding independently. Fruit production which is maintained until the beginning of the dry season, in April/May, permits species such as *Cheirogaleus medius* and *Microcebus murinus* to accumulate fat reserves preceding the period of lethargy (Chapter 6).

Young leaves are also an important potential food resource (A. Hladik, 1978) and are partly used by Cheirogaleinae before fruits become abundant. By contrast, tough mature leaves are potential food for *Lepilemur ruficaudatus* only. The major importance of leaf production is the direct impact on invertebrate production (see below) which is of paramount importance for most species of nocturnal prosimians.

Composition of Plant Parts

Samples of prosimian foods were collected in the Marosalaza forest, and preserved for analysis according to standard techniques (Hladik, 1977c). Results of the analysis of the major types of food are presented in Table I.

Since flowers and fruits are likely to provide the staple food of various prosimian species during long periods, their relative composition of carbohydrates and protein might be determinant of the dietary balance. In this respect, it is remarkable that the mean protein content of the different fruit samples (7.3%) is high compared to that of the fleshy parts of most fruits of the African rain forest and the Asian semi-deciduous forest (rarely in excess of 5%; Hladik, 1977b; 1978a). For animals feeding on insects and fruits, the risk of facing protein deficiency during periods of insect scarcity is thus lower than in other environments. For example, the protein-rich fruit of *Operculicarya gummifera* (7) which is also rich in fat, is a highly valuable food for *Cheirogaleus medius* at the beginning of its period of activity. This animal feeds on the pulp of such fruits and disperses the seeds in feces, and consequently exerts a selective pressure in favor of the most attractive fruits in terms of nutrient. Although this is a general phenomenon (see discussion in Chapter 1), selection pressures are influenced by the long dry season in the Marosalaza forest, which results in a decrease of most food resources (especially protein, i.e., insects; see below), and explains the unusually high protein content of fruits (Table I).

Gums and tree exudates have a very low protein content which implies the necessity of a protein supplement (insect) for species feeding on these resources. One sample of gum of *Terminalia tricristata* (49) presents a high content of soluble sugar extracted after weak hydrolysis. This appears surprising, because in other samples of gum (mainly those of lianas and trees of Gabon), the same type of hydrolysis does not break the apparently

TABLE I

Composition of Samples of Foods Eaten by Prosimians[a]

Type of food	Percentage dry weight: Protein ($N \times 6.25$)	Percentage dry weight: Reducing sugars (after weak hydrolysis)
Flower extract		
Delonyx floribunda H. 14 A (38)	6.4	68.2
Fruits (fleshy parts only)		
Operculicarya gummifera H. 3 A (7)	9.5	14.2
Physena sessiliflora H. 53 A (85)	8.3	32.5
Strychnos decussata H. 25 A (93)	7.1	55.9
Grewia glandulosa H. 52 1 (168)	6.0	15.8
Evonymus plurostyloïdes GP. A (43)	5.8	17.1
Gums		
Terminalia mantaliopsis PCD. 3 F (48)	5.2	
Terminalia tricristata H. 58 F (49)	3.3	
Terminalia tricristata EP. 3 S (49)	2.6	87.8
Other tree exudate		
Sap of *Adansonia fony* PCD. 2 F (20)	5.1	
Insect secretion		
Dried secretion from larval colony of *Flatida coccinea* EP. 1 S	1.4	5.0

[a] Collected in the Marosalaza forest by P. Charles-Dominique (PCD.), C. M. Hladik (H.), E. Pages (EP), and G. F. Pariente (GP.). The reference numbers in parentheses are those in Appendix I in Chapter 1.

strong chains of pentoses (C. Mercier, personal communication, and unpublished data of C. M. Hladik and Charles-Dominique), and in these cases, only a small amount of soluble sugars is obtained. This type of analysis of soluble sugars has been chosen (Hladik *et al.*, 1971) to account for what is likely to be assimilable by most mammals without a particular digestive adaptation. Accordingly, some of the gums available in the Marosalaza forest appear to be readily digestible by nonspecialized prosimians. The specialized gum eaters might thus have originated from this type of forest; but further investigation should be necessary to confirm this hypothesis.

The investigations concerning the possible toxicity of plants in the Marosalaza forest have been limited to the alkaloid screening of Hladik (Chapter 1). Other secondary compounds, such as tannins, glycosides, and saponines, may also be toxic (Whittaker and Feeny, 1971) and were actually found in some of the samples from the West Coast of Madagascar analyzed by Debray *et al.* (1971). The overall results of the alkaloid survey indicate concentration of alkaloids mainly in evergreen species. This may reduce the possible food choices for a folivore such as *Lepilemur ruficaudatus* during the dry season. In contrast, the other prosimian species feeding on fruits and nectars are not expected to face plant toxicity.

Invertebrate Production

Sampling invertebrate production in order to determine what is available as food to prosimians, necessarily implies a bias due to the method of collection. An ultra violet lamp located near the forest border was used to attract flying insects in a trap, during 2 hours at the beginning of each night. After the initial period of intense capture (> 25 gm dry weight, per night), the "production," including mainly Coleoptera, was more stable and probably reflected variations of a part of the invertebrate food available to nocturnal prosimians. The amount of insects progressively increased from January to February (from 6 to 15 gm), and subsequently tended to decrease (about 8 gm in March). This insect population thus followed the pattern of leafing of most trees illustrated by Fig. 1, the insects being available about 2 months after the leaves have developed.

A more reliable estimate is provided by caterpillars' feces collected and weighed in the litter (Table V, Chapter 1). The increase of caterpillar feeding activity is also subsequent to leaf growth with a maximum reached in May. It thus can be assumed that insect populations attain maximum density at the end of the rainy season.

Accordingly, the food available to most nocturnal prosimians, which is mainly composed of carbohydrates (nectars) in November, and includes fruits with a fairly high protein content in December/January, would progressively become richer in insect protein in February/March (insect composition includes approximately 70% protein, dry weight; Hladik, 1977b). The continuation of fruit production in March/April (Fig. 1) would subsequently result in a diet including more carbohydrates for the species which increase food intake before the dry season.

Invertebrate availability was not homogeneous in the study area, especially during the dry season. Different samples collected by E. Pages showed that the amount of arthropods was twice as large in the dense vegetation around the temporary pond as in the dryer parts of the forest (Table II). The distribution of invertebrate populations is also influenced by forest structure, for example, Orthoptera are present in larger quantity in Area 3. An extrapolation from these results and leaf production indicates an order of magnitude of 0.5 to 1.0 kg per hectare of invertebrate biomass.

TABLE II

Comparison of Arthropod Samples Classified According to Possible Level of Identification, in Different Areas of the Marosalaza Forest[a]

	Number of individuals (percentage occurrence)	Dry weight (gm)	Percentage of dry weight
Area 1			
Arachnids	55(53)	0.16	30
Blattaria (cockroaches)	24(23)	0.12	23
Mantiidae	7(6)	0.08	15
Coleoptera	5(5)	0.04	8
Hemiptera	4(4)	0.04	8
Homoptera	4(4)	0.03	6
Lepidoptera	2(2)	0.03	6
Orthoptera (crickets)	1(1)	0.01	2
Hymenoptera	1(1)	0.01	2
Area 2			
Arachnids	56(55)	0.21	41
Blattaria	22(21)	0.08	15
Orthopthera	5(5)	0.05	10
Lepidoptera	3(3)	0.05	10
Homoptera	7(7)	0.04	8
Mantiidae	4(4)	0.04	8
Misc. including ants	5(5)	0.04	8
Area 3			
Blattaria	38(26)	0.28	27
Arachnids	74(50)	0.26	25
Orthopthera	8(5)	0.22	21
Hemiptera	13(9)	0.12	12
Lepidoptera	8(5)	0.08	8
Coleoptera	4(3)	0.04	4
Homoptera	5(3)	0.02	2
Hymenoptera	4(3)	0.01	1

[a] The samples were collected by E. Pages from the leaves of *Buxus madagascariensis* collected at random up to 5000 gm fresh weight. The three areas investigated (Area 1 along trails A to M; Area 2 along trails M to R; Area 3 along trails R to W) have also been compared for population density of *Microcebus coquereli* (see Chapter 4, Table I).

Other types of invertebrates are not directly preyed upon by prosimians but nevertheless play a role in producing secretions available as food. Different cochineals have been observed as well as homopterans. The most abundant species is *Flatida coccinea* (Homoptera, Fulgoridae; Fig. 3)* which forms large colonial aggregates on the vine *Elachyptera minimiflora*

* Identification was made by M. Boulard (Laboratoire d'Entomologie, Museum National d'Histoire Naturelle).

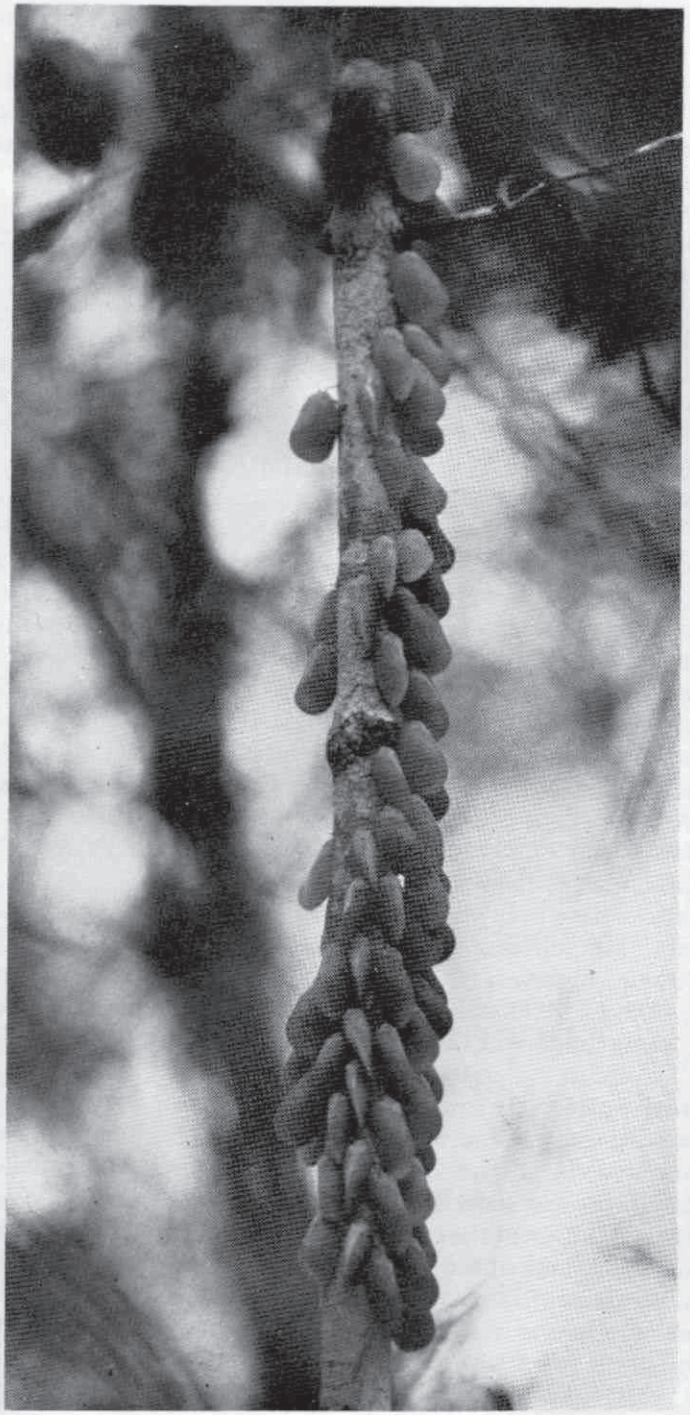

Fig. 3. The homopteran, *Flatida coccinea*, feeding on a stem of the vine *Elachyptera minimiflora* during austral summer. At the larval stage, during the dry austral winter, these insects secrete large quantities of honey dew available as food to *Microcebus coquereli* (photo by C. M. Hladik).

(88). During the dry season, the larval forms produce large droplets of honey dew which may be licked by *Microcebus coquereli* (see Chapter 4). This secretion falls on the leaves under the colony, and dries to form a white sweet concretion which remains edible. Results of analysis of this product are shown in Table I. The very low protein content is not surprising since the plant sap extracted by the insect is initially poor. In addition, the low value of reducing sugars is probably due to a nonreducing component which has been described as "mannite" (Decary, 1946) and was exploited by humans.

Vertebrates, mainly chameleons which appeared to be abundant in the Marosalaza forest, also form a part of the food available for prosimians.

POPULATIONS OF NOCTURNAL PROSIMIANS IN RELATION TO FOOD AVAILABILITY

Population censuses were conducted in 1973 and 1974, in the study area of the Marosalaza forest (see Fig. 5, Chapter 1). The animals were captured and consistently recaptured in spring-loaded traps, and marked with different combinations of ear cuts and complementary visible marks by depilation of some parts of the tail, according to the different methods of Charles-Dominique (1977). These data (Table III) are the most reliable, since the nocturnal observations conducted during several months showed that most of the animals present in the center of the study area consisted of marked individuals. In species for which home ranges have been measured (see Chapters 3 and 4), the densities indicated in Table III have been calculated according to these measures.

Other censuses have been made along transects, in order to obtain comparative data from different areas (Table IV). These were conducted repeatedly by two observers (C. M. Hladik and P. Charles-Dominique in November, 1973; C. M. Hladik and G. F. Pariente in January, 1974) walking slowly along trails with headlights, and using a measuring device ("Topofil") to locate accurately all observations. In a given area, successive surveys yielded very similar results.

Population densities of the different prosimian species have the same order of magnitude in different parts of the closed forest. These densities are extremely high, especially for *Cheirogaleus medius* and *Microcebus murinus* (Table III). One of the transects in the closed forest (Table IV) was located about 5 km south of the study area (a trail previously opened for oil prospection was reused). The lower densities calculated in this case for *C. medius* and *M. murinus* may well be due to the poor visibility in the undergrowth of the forest where these species generally forage. On the contrary, the population densities of *Phaner furcifer* and *Lepilemur*

TABLE III

Population Densities and Biomasses of Nocturnal Prosimians in the Study Area[a]

	Cheirogaleus medius	*Microcebus murinus*	*Microcebus coquereli*	*Phaner furcifer*	*Lepilemur ruficaudatus*
Number of animals:	31	72	9	14	4
Area controlled (ha)	(9)	(20)	(30)	(25)	(2)
Estimated population per km² (100 ha)	350	400	30	50–60	250
Biomass (gm/ha)	500–700	200	100	200	2000

[a] Marosalaza Forest, 50 km north of Morondava.

TABLE IV

Comparison of Population Densities in Two Different Areas of the Forest of the West Coast of Madagascar

	Cheirogaleus medius	*Microcebus murinus*	*Microcebus coquereli*	*Phaner furcifer*	*Lepilemur ruficaudatus*
Transect in closed forest (3 ha); Number of animals	6	2	1	3	10
Estimated population per km²	200	60	30	100	330
Trail from closed forest to Sira Sira (4.4 ha); Number of animals	1	6	0	2	2
Estimated population per km²	20	130	0	40	40

ruficaudatus are certainly exaggerated as a consequence of the excellent visibility in the tree tops where records were possible at distances exceeding 15 m from the trail (see methodological discussion about "visibility profiles" in Charles-Dominique and Hladik, 1971). Nevertheless, this method of census showed clear-cut differences between the closed forest and the transitional part on dry and/or salty soils towards the "Sira sira," where *Microcebus coquereli* is totally absent. The low population densities of the other species along this transect (Table IV) indicate a gradation in which most animals have a normal density near the tall forest, which diminishes fairly abruptly towards the Sira sira. The two exceptions are *M. murinus,* that we observed in low bushes up to the extreme limit of the Sira sira, and *P. furcifer* which probably can survive on a shrub producing gums, closely related to the "Talys." The local decrease in population densities can be related to the obvious scarcity of food resources in the lower less dense parts of the forest.

Biomasses and Food Availability

The biomasses of the different prosimian species, which have been calculated according to population densities (Table III), are the best "transducers" of the possible feeding strategies. The classical approach of any ecosystem through a pyramid of the biomasses (Odum and Odum, 1959) has been refined by a classification of primate species into "dietary grades" (Hladik, 1975; Hladik and Chivers, 1978) which are sorts of intermediate levels in this pyramid, and correspond to particular dietary types. These grades are: animalivore (grade 1) presenting a gradual frugivorous tendency towards an intermediate type (grade 2) in which protein balance is obtained from a mixture of animal prey and plant parts, and the folivore/frugivore type (grade 3), exclusively vegetarian. The different levels in these three grades can be expressed by the logarithm of the biomass (in grams per hectare), from 1.0 (grade 1 with biomass 10), up to 3.9 (grade 3 with biomass smaller than 10,000). The interdependence between biomasses and dietary types is due to a fairly homogeneous production of the different food types in the tropical forests throughout the world (see A. Hladik, 1978; C. M. Hladik, 1980).

According to Table III, most nocturnal prosimian species are in grade 2 *(Cheirogaleus medius:* 2.8; *Microcebus murinus:* 2.3; *Microcebus coquereli:* 2.0; *Phaner furcifer:* 2.3). Only *Lepilemur ruficaudatus* is in grade 3. Prosimian species must thus depend to a large extent on plant food resources (see below, and Fig. 10), but the system of sharing plant production might be delicate, since the average production (about 3 tons/ha/year

in terms of dry litter fall; Chapter 1) is one of the smallest among tropical forests.

Furthermore, the Marosalaza forest not only supports the total biomass of 3100 gm per hectare of nocturnal prosimians, but an even larger biomass of diurnal lemurs as well. The two diurnal species, *Propithecus verreauxi* and *Lemur fulvus,* have been briefly observed. Probably due to recent hunting pressures these species seem less abundant as compared to the more accurate records of Jolly (1966), Richard (1974), and Sussman (1974), obtained in southern areas supporting types of deciduous forest comparable to Marosalaza. Nevertheless, *L. rufus* and *P. verreauxi* are sympatric with *Lemur catta* in these other areas, and we might expect at least a few changes in their feeding strategies, due to the absence of a potential competitor for food resources in Marosalaza. Tree and liana leaves and fruits were used to a large extent, for instance the genera *Landolphia* (8), *Cordyla* (36), *Grewia* (168–173) by *L. rufus,* and *Cynanchum* (12), *Diospyros* (55–60) by *P. verreauxi.*

Cynanchum (12), *Diospyros* (55–60) by *P. verreauxi.*

The total biomass of prosimians utilizing the plant production of the Marosalaza forest is thus very high (between 6,000 and 10,000 gm/ha). It has indeed the same order of magnitude as in other tropical forests affected by important seasonal changes, such as the gallery forest of the south of Madagascar (Jolly, 1966; Charles-Dominique and Hladik, 1971), or the Wilpattu forest in Sri Lanka (Eisenberg *et al.,* 1972; Hladik and Hladik, 1972). However, in Marosalaza, production is significantly smaller, and the seasonal variations in food production and composition appear more important than in these forests. The diversification of the feeding strategies of the different prosimian species seems to be a response to these environmental constraints.

ADAPTIVE STRATEGIES OF PROSIMIANS

Hibernation: The Fat-Tailed Dwarf Lemur, *Cheirogaleus medius*

The most characteristic feature of *Cheirogaleus medius* is the ability to hibernate for at least 6 consecutive months and, in some instances, up to 8 months of the dry season. During this period, the animals remain totally inactive. They retire inside deep holes of tree trunks where three to five individuals may be piled upon each other, separated by a kind of soft lodge made of wet decaying wood.

Fig. 4. A group of *Cheirogaleus medius* at the beginning of the rainy season, just emerging from the hollow trunk where they have been hibernating (photo by C. M. Hladik).

In the Marosalaza forest, the Fat-Tailed Dwarf Lemurs were first observed to emerge from their holes (Fig. 4) and forage at night at the end of November, just before the first rain started. Accordingly, as can be seen in Fig. 1, the animals are active exclusively during the period of intensive food production. Since populations of other nonhibernant prosimian species are limited by temporary reduction of food resources, *C. medius* can be considered as feeding mainly during the temporary period of *surplus* food.

Diet

The diet of *C. medius* was determined by direct observations at night, and from the analysis of fecal material collected when the animals were caught for marking. In this analysis, the baits used in the traps (bananas) were mixed with the other materials, but the remains of animal matter allowed a comparative study of the diets of different prosimian species captured in similar conditions.

Fruits formed the staple food (together with flowers in the beginning of the period of activity). Invertebrates were present in 50% of the feces, but in small amounts, the volume of chitin never exceding 10% of the other food remains. Coleoptera were the major type of prey (also observed: cockroaches, ants, cochineals, Cicada (?), and other undetermined invertebrates). The skin of chameleon was also found in one feces sample.

The small number of samples (31) did not permit following of the seasonal food cycle, but indicated an increase of invertebrate food in January, corresponding to the apparent increase of insect populations (see above). *C. medius* has been observed foraging for insects at medium height (4–8 m) in the Marosalaza forest.

The seeds of small fruits were intact in feces, mainly those of *Operculicarya gummifera* (7) and *Grewia glandulosa* (168), but the animals were also observed to eat pulps of larger fruits such as *Strychnos decussata* (93) and *Diospyros aculeata* (55), in December.

Flowers were licked and may form an important food supply. For instance, the nectar of the Boy flower, *Delonix floribunda* (28) (Fig. 2), seemed to be the unique food of one individual (♀8) followed by radiotracking during 6 consecutive days in December. The animal moved from a nearby tree hole to the large Boy tree covered with flowers, and retired after a relatively short period of active feeding. Flowers of *Baudouina fluggeiformis* (31), a common small tree, were also frequently visited.

Some gums may be used (found in fecal samples) as well as many other plant or insect exudates (direct observations). When the animals licked leaves, it was difficult to identify the type of secretion (homopteran, cochineal, or nectar from flowers). Tender parts of plants may also be eaten in small amount.

In general, *C. medius* appears as an opportunistic frugivore complementing its diet with the most abundant and nutritious food types. The seasonal variation in diet follows food availability: nectars and fruits in November; fruits and an increasing proportion of insects in December/January/February. After this period, the proportion of fruits might be higher in the diet at the time of fattening preceding hibernation.

Variations in Body Weight

Capture, marking, and recapture of 31 *C. medius* permitted the recording of the overall variations in body weight in Marosalaza forest (Fig. 5). During the active period, the animals accumulate large fat reserves under the skin and inside the tail (Fig. 6). Adult mean body weight varied from 142 gm in November to 217 gm in March. The tail volume was measured by immersion (after wetting) in a graduated cylinder filled with water. Maximum adult tail volume (56 cm^3) was observed in May before hibernation, and minimum (9 cm^3) in November, after hibernation, the monthly means being, respectively, 42 cm^3 (SD = 9) and 15 cm^3 (SD = 4).

Similar body weight variations of *C. medius* have been subsequently recorded in artificial conditions (Chapter 6), but the period of "inactivity" was not as marked as in natural conditions (no true hibernation), and the

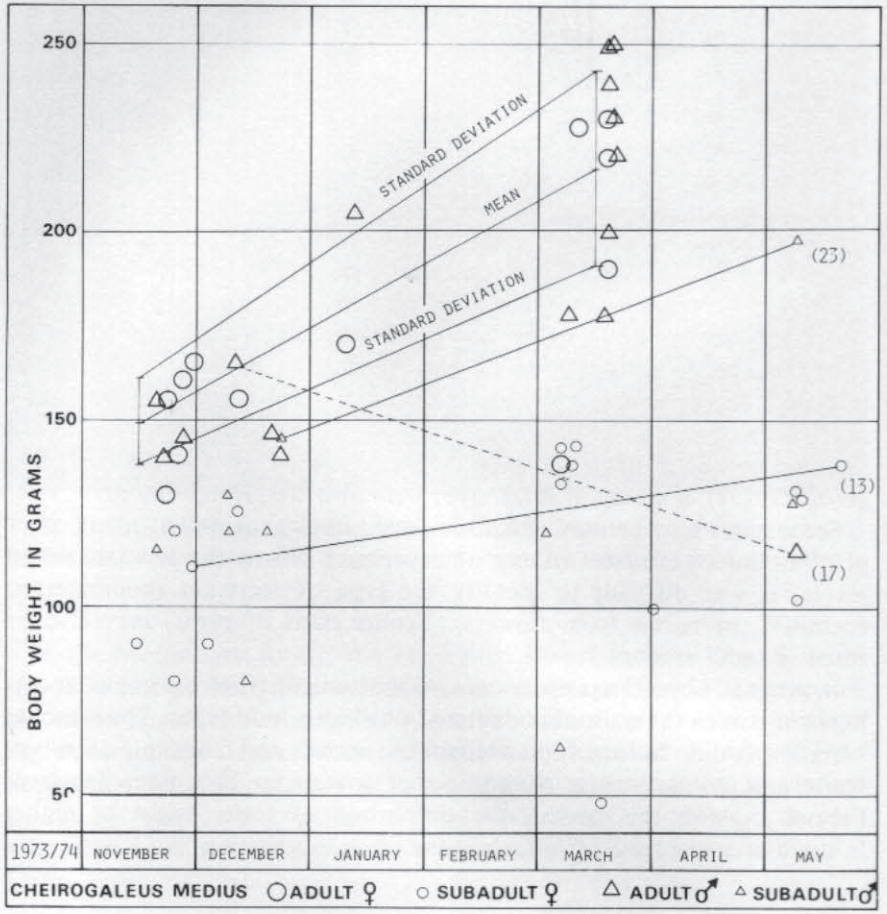

Fig. 5. Seasonal variation in body weight of *Cheirogaleus medius,* in the Marosalaza forest, according to data of captured and recaptured marked animals. The increase in adult body weight from November to March can be seen by the mean and standard deviation from 142 gm (SD = 12) to 217 gm (SD = 26). Note the important individual scatter in March, due to local conditions and/or individual status. The young animals (born in 1973/74) have the smallest weight. Individual data show growth of one subadult male (23), that of one subadult female (13), and that of an adult male (17) who lost weight (broken line) and was probably unable to survive the next dry season. Except for this last animal, only subadults were caught in May (adults began hibernating in March).

loss of weight less important. Nevertheless, these detailed records permitted the progressive changes in the patterns of food intake to be followed. There is a very marked increase of food intake concomitant with a decrease in activity preceding the period of lethargy. Furthermore the food choices were

Fig. 6. *Cheirogaleus medius* illustrating variations in tail volume. (A) The maximum size of tail, due to fat accumulation (photo by J. J. Petter). (B) The minimum tail volume, observed in November, just after hibernation in the Marosalaza forest (photo by A. Schilling).

oriented toward different food categories according to the period of the active cycle (Chapter 8).

These important variations in behavior and/or physiology can be interpreted according to the variations occurring in the wild, since they follow a similar overall pattern. At the beginning of the active period, when the food available was mainly carbohydrates (nectars and fruits), the animals tended to direct food choices toward this type of food (even when other types were available in artificial conditions). Dietary increase in protein which was due to insect availability in the Marosalaza forest also occurred in artificial standard conditions during the corresponding period of the annual cycle. Finally, the period preceding lethargy was marked by a diet rich in fruits for the animals in their natural environment, as well as for those studied in artificial standard conditions.

As a matter of fact, it appears that the feeding behavioral tendency of *C. medius* varies throughout the year and seems "preadapted" to the important changes of the natural environment (see discussion in Chapter 8).

Some other important changes in the apparent coefficient of food assimilation also precede the period of lethargy (Chapter 9).

The variations in body weight shown in Fig. 5 are thus related to successive adaptations in physiology and behavior, the most important being the sudden change in food choice, food intake, and overall activity, which precedes hibernation.

Reproduction

Mating was observed at the beginning of November, as soon as *C. medius* resumed activity after hibernation. Births occurred in January, at the time of increasing food availability.

Young animals have a relatively low body weight in March (Fig. 5) and continue to feed until May. At this time all the adults are already hibernating and thus do not compete for the remaining available food. The period of hibernation is consequently shorter for these young, and their loss in weight may be limited. Their lacteal last premolar is still present during this first hibernation, and is replaced only at the beginning of the next period of activity during which they attain the adult body weight.

Home Range

Most of the 31 marked *C. medius* did not move over ranges exceeding 200 m in diameter (about 4 ha). Larger displacement during the whole period of activity are generally by juveniles. Considering the very high population density (Table III), the ranges of the different adults must necessarily have important overlaps.

No detailed information concerning territoriality in this species could be obtained by direct observation during the wet austral summer. In captivity, individuals are generally intolerant to individuals of the same sex. The fecal marks which are very abundant, especially before the period of hibernation (Chapter 9), are likely to play a role when the animals resume activity.

Since no important movements were recorded at the beginning of the active period, except for two adults of small body weight (peripheral males?), it may be concluded that most adult *C. medius* stay in the same area during successive years.

The imperative necessity to find a shelter for hibernating seems as important as food resources for *C. medius*. It has been stressed (Chapter 1) that a remarkable aspect of the forest of the West Coast of Madagascar is the high frequency of hollow trunks in many common species such as the Anatsiko, *Securinega seyrigii* (79), the Harofy, *Commiphora* spp. (24/25), and the Iron wood, *Strychnos decussata* (93). This was a necessary condition

permitting the emergence of the feeding strategy of *C. medius* which consists of harvesting "surplus" food when available, and withdrawing during the period of minimum production.

Reduction of Activity: The Lesser Mouse Lemur, *Microcebus murinus*

Microcebus murinus is not a true hibernant, but is comparable to *Cheirogaleus medius* by its period of lethargy (Chapter 6) which also occurs during the dry season. At this time, the animals may stay in hollow trunks for several consecutive days, and their overall activity is considerably reduced. Nevertheless, *M. murinus* are visible at night in the forest at any time of the year.

Feeding activity of the Lesser Mouse Lemur is thus maintained throughout the year, but decreases during the dry austral winter. At this time of reduced food availability, only small amounts are actually necessary, as was the case for the juvenile *C. medius,* the active period of which is longer than that of adults. The major proportion of annual food intake of *M. murinus* coincides with maximum fruit and insect production (austral spring and summer). Accordingly, the basic strategy of this species is to rely on this excedent in available food.

Diet

The diet of *M. murinus* appears to be fairly similar to that of *C. medius*. Since the two species mainly feed on the same seasonal stock of "surplus" food, a more detailed analysis of food choices and of other behaviors related to feeding activity is necessary to explain the persistence of both species in this particular food niche.

Fruits form the staple diet of *M. murinus,* but are complemented with a higher proportion of animal matter than for *C. medius*. Chitin was present in all fecal samples of *M. murinus* trapped in the Marosalaza forest, and again Coleoptera were the most abundant insect food. Feces of at least one animal (which had no time to digest the bait used in the trap) were exclusively composed of chitin. Direct observations provided evidence of active predatory behavior directed toward rapid prey such as moths, crickets, and cockroaches. We also observed a chameleon devoured in small pieces during a period of 20 minutes. It is not surprising to find in the diet of *M. murinus* a relatively larger proportion of insects than in that of the larger *C. medius,* because, on the average, both species collect approximately the

same absolute quantity of animal prey (cf. Hladik and Hladik, 1969; Charles-Dominique, 1977, for discussion on insect and fruit eater).

Together with the more rapid movements allowing capture of flying insects, the foraging habits of *M. murinus* (Fig. 7), exclusively observed in the dense undergrowth (at 1.5–6 m), tend to reduce interspecific competition between these two Cheirogaleinae, because they prey on partly different invertebrate populations.

Nectars and the exudates of plants and insects were fed upon in an opportunistic manner. Accordingly, the diet includes certain typical foods of *Cheirogaleus, Phaner,* and *M. coquereli* (see below). Green vegetal material

Fig. 7. *Microcebus murinus* foraging in the undergrowth of the Marosalaza forest.

was also occasionally included in *M. murinus* diet, as was previously observed by Martin (1973) in the south of Madagascar. A differential utilization of flower nectar and pollen may be due to plant morphology. For example, the Maronono, *Evonymus pleurostyloides* (43), a small tree, bears large bunches of flowers emanating from the trunk near the ground. These flowers were visited frequently in December/January during the different bouts of foraging activity always occurring at low level. The fruits of this tree, available in March, were eaten as well (G. F. Pariente, personal communication).

The seasonal variations in dietary composition of *M. murinus* appear to be roughly similar to those of *C. medius,* and depend on variations of food availability; but the increase of protein intake in spring and summer is more important.

Variations in Body Weight

The records of body weight of 72 recaptured *M. murinus* are presented in Fig. 8. Annual variations, although smaller than for *C. medius,* are still very important. Fat is accumulated under the skin and in the tail during the austral spring and summer. However, the tail fattening of *M. murinus* is never as spectacular as in the peculiar case of *Cheirogaleus.* Maximum variations recorded in the Marosalaza forest were from 2 to 9.5 cm^3. In captive conditions, *M. murinus* were fatter, and tail volume varied from 5 to 20 cm^3.

As in the preceding case study, the observations of captive animals during several years allowed a better understanding of the behavioral and physiological cycles. The period of increased food intake of *M. murinus* in artificial conditions occurred about 2 months after that of *C. medius* and was also preceded by a reduction of overall activity (Chapter 6). In these experimental conditions, fattening was followed by a type of lethargy which seems almost identical to that observed in the Marosalaza forest. Further observations on food intake (Chapter 8) also showed a variation in the propensity for different dietary components, according to the period of year.

In spring and summer, the diet of *M. murinus* included more protein as soon as insects were available in the Marosalaza forest. Similar variation in protein content of the overall diet was also observed during artificial food choices in standard conditions. The opposite dietary tendency (a diet rich in carbohydrates) appeared before the period of lethargy.

From December to May, the body weight variations resulting from these successive changes in feeding behavior of *M. murinus* (Fig. 8) are more

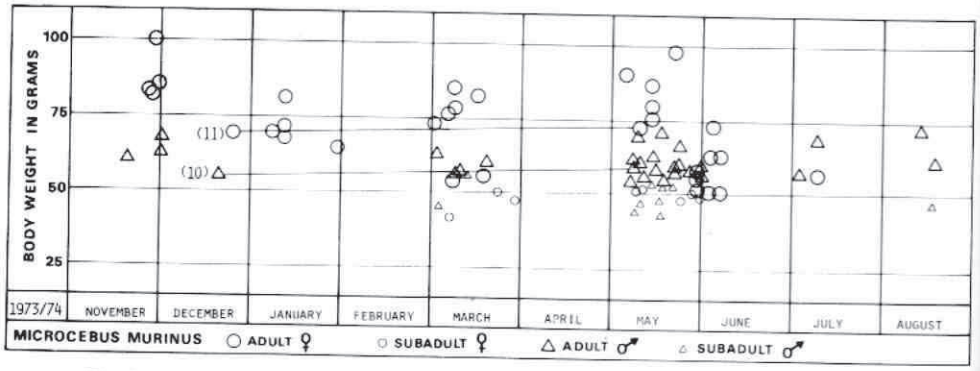

Fig. 8. Body weight of *Microcebus murinus* in the Marosalaza forest. The seasonal variation of body weight is smaller than that of *Cheirogaleus medius* (compare with Fig. 5). Individual variation is shown by solid line for one adult male (10) and one adult female (11).

progressive than for *C. medius*. The abrupt body weight increase following dietary variation, which was observed in autumn in artificial conditions only, probably also occurs in the wild and might explain the apparent scatter of the data collected in May (austral autumn) in the Marosalaza forest.

Protein intake from a standard diet was always larger for *M. murinus* (mean: 11.6%) than for *C. medius* (mean: 9.2%). This reflects the conditions in the Marosalaza forest where ecological mechanisms determine the possible diet for each species according to body weight and food availability. It also implies physiological and/or behavioral systems which are a sort of "preadaptation" directed towards the adequate food choices.

In addition to these variations in body weight, food intake, and food composition, which also depend on variations of the basal metabolism, Perret (1979) recorded a diminution in water intake during a period corresponding to the dry season. This appears as another kind of variation in physiological parameters which can be qualified as preadaptation to the environmental changing conditions.

Population Parameters

Population density of *M. murinus*, which approximates four animals per hectare (Table III) has the same order of magnitude as in other dry forests of the south of Madagascar (Charles-Dominique and Hladik, 1971). Thus, due to small body weight, the biomass of *M. murinus* is smaller than that of *Cheirogaleus medius*. For both species, the carrying capacity of the environment is likely to be determined by insect food availability, and the larger the insect component in the diet, the smaller the biomass.

According to our data on capture, recapture, and localized direct observation of marked animals, we only can suggest that the home range does not excede 150 m in diameter (about 2 ha) in the Marosalaza forest. In the more humid forest of the southeast of Madagascar where Martin (1973) carried out similar observations, the home range of *M. murinus* appeared to be smaller, possibly due to more important food availability. In these conditions, social structure involved "population nuclei" based on females, and the presence of "central males" with a relatively high body weight in spite of annual variation, and "peripheral males" of relatively lower body weight. A similar organization is expected to be found in Marosalaza.

Utilization of Insect Secretion: The Coquerel's Mouse Lemur, *Microcebus coquereli*

In contrast to precedent species of Cheirogaleinae, *Microcebus coquereli* shows little annual variation in food intake and body weight (body weight range: 280–335 gm in captured animals). Population density and biomass are consequently low as compared to those of other species (Table III), because the carrying capacity of the environment is determined by minimum food availability during the dry season. The species is adapted in an unusual manner to a peculiar food which remains available throughout the dry season: insect secretion. This was first described by Petter *et al.* (1971). A more detailed study of the population of *M. coquereli* of the Marosalaza forest is presented by Pages (Chapter 4). A few complementary points will be presented in order to stress the differences with sympatric prosimians in terms of feeding strategy.

Diet

According to the frequency of chitin in fecal samples, *M. coquereli* seems to be as insectivorous as *M. murinus*, and also eats large amounts of fruits (only one sample out of seven contained fruits only and no chitin). However, the liquid part of the diet cannot be measured or even detected in fecal samples. Only direct observation permitted an estimate of the importance of this food in terms of feeding frequency or time-budget. For in-

stance, during the dry season *M. coquereli* was most frequently seen licking the secretion of the colonial aggregates of *Flatida coccinea* (up to 50% of the feeding observations of Pages, Chapter 4, and 60% of the feeding time). As a matter of fact, even in austral spring and summer, the Coquerel's Mouse Lemur ate many kinds of insect secretions (from cochineals and homopterans) as well as plant exudates, including gum of *Terminalia* spp. (48/49). For example the Fangoky, *Delonix boiviniana* (37), was frequented when flowering, the animals licking flowers (nectar) as well as leaves (cochineal exudate?).

Animal foods are of paramount importance because plant exudates and insect secretions have an extremely low protein content (Table I). The data of Pages (Chapter 4, Table I) also suggest that invertebrate food availability determines the distribution of *M. coquereli* in the study area. Vertebrate prey are also frequent, as shown by the skins of chameleons found in two out of seven feces samples. In captivity, *M. coquereli* eat young mice and any kind of mince meat. In fact, an unfortunate involuntary experiment at the Brunoy animal house showed that *M. murinus* can be preyed upon by *M. coquereli* if they are introduced into the same cage. In natural conditions, *M. coquereli* forages at relatively low levels (about 5 m in height), but it is likely that *M. murinus,* thanks to its small size and vivacity, can escape in the dense undergrowth or in small tree holes. As in most cases, predation might only concern a marginal part of the population (very young, or old animals).

Seasonal Cycles

As with other prosimian species, there are seasonal changes in the diet of *Microcebus coquereli* depending on food availability. The honey dew of *Flatida coccinea,* which is intensively consumed during the dry season, is exclusively secreted by larvae. In December/January, these Homoptera reach their imaginal stage (Fig. 3) and are no longer visited. At this time, the types of food also utilized by other prosimians (fruits and insects) are eaten. Accordingly, the diet of *M. coquereli* is subject to partly similar variations.

The variations recorded during the study of food intake in artificial conditions (Chapter 8), although of lesser importance than for other species, followed a significant pattern which evokes field conditions: a relative decrease of protein-rich foods in autumn and winter resulting from a diet mainly based on soluble carbohydrates, and the progressive increase of more nutritious foods (protein and fat) in spring. As for other species, this seasonal variation of the "dietary tendency," which was maintained even

in standard and homogeneous conditions, appears as an adaptation to the extremely important variations in composition of the food available in the forest of the West Coast of Madagascar.

Utilization of Gums: The Fork-Marked Lemur, *Phaner furcifer*

Phaner furcifer has approximately the same body size as *Microcebus coquereli,* and is also able to face the dry season without apparent variation in body weight and no evident change of the activity pattern and/or basal metabolism. Nevertheless, there is no significant competition during the dry season for the staple food of each species since *P. furcifer* is highly specialized on gum and other tree exudates, as was shown by Petter *et al.* (1971), and more recently observed in the Marosalaza forest by Charles-Dominique and Petter (Chapter 3). Different plant exudates and insect secretions can actually be eaten by both *P. furcifer* and *M. coquereli,* but behavioral and/or physiological specialization result in a definite interspecific difference in dietary preference.

As in the preceding case, the staple food which is relatively poor in protein, has to be complemented with animal food (mainly insects). Every night, *P. furcifer* forages for insects during long periods but always subsequent to an initial period of gum feeding (Chapter 3). The selection of prey is different than that of *Microcebus coquereli;* in particular, no vertebrates are eaten. Foraging also occurs at a higher level (8–10 m, and often in the tree tops). Interspecific competition is thus reduced, but, as for *M. coquereli,* the carrying capacity of the environment is probably determined by insect food availability. The relatively important biomass of *P. furcifer* in the Marosalaza forest (about twice as large as that of *M. coquereli;* Table III), may result from the relative protein richness of the gum of *Terminalia mantaliopsis* (48) as compared to insect exudate (Table I). This gum necessitates a smaller proportion of insects (about 10%) in the diet of *P. furcifer.*

In captivity (see Chapter 8), the artificial diet was probably too different from that in nature to allow a normal physiological cycle. No obvious seasonal pattern was observed.

Phaner furcifer has no imperative necessity to find hollow trunks for protection during the dry season (as for *Cheirogaleus medius,* see above). Nevertheless, the number of adequate hollow trunks to use as day nests may be limited, due to occupation by a large number of *Lepilemur ruficaudatus.* As a matter of fact, *P. furcifer* was so frequently found in

the abandoned nests constructed by *M. coquereli* during the first survey of Petter *et al.* (1971) that it was not possible to distinguish which species was responsible for nest construction.

Folivory: The Sportive Lemur, *Lepilemur ruficaudatus*

The very high biomass of *Lepilemur ruficaudatus* (body weight about 900 gm, Fig. 9) in the Marosalaza forest (Table III) is obviously related to the ability of the animal to utilize the most ubiquitous food resource: leaves.

In the fecal samples collected during the austral summer, leaf fiber was mixed with the seeds of fruits, especially those of *Diospyros* spp. (55/56), but leaves always constituted the staple food. During the austral winter, the limited number of evergreen species, and the frequency and high amounts of alkaloids present (see Chapter 1) may reduce the possible food choices of *Lepilemur ruficaudatus*. In practice, leaves and/or flowers of one or two species may be sufficient to supply the Sportive Lemur population during

Fig. 9. *Lepilemur ruficaudatus* in the Marosalaza forest (photo by C. M. Hladik 1201 P).

several dry months, as was demonstrated for *L. leucopus* (Charles-Dominique and Hladik, 1971).

In all species of *Lepilemur* thus far studied, caecotrophy is observed (Hladik and Charles-Dominique, 1974; C. M. Hladik, 1978a), which allows sufficient efficiency in digestion of long-chain β-linked carbohydrates. *Lepilemur ruficaudatus* was also observed in the animal house of Brunoy reingesting "feces" at various intervals, during the quiet period of artificial daylight.

The survey of food intake in artificial conditions (Chapter 8) showed a definite seasonality. As in the case of the other nocturnal prosimians subject to important seasonal changes, there was an increase of the proportion of fruit included in the diet during spring and summer. Although the annual variation of body weight and activity is not very marked (Chapter 6), *L. ruficaudatus* appears to be "preadapted" through a seasonal shift in feeding behavior, to include a larger proportion of fruits in its diet at the time of maximum availability.

The reproductive cycle (Chapter 6), which differs from that of the sympatric species, also permits an adequate utilization of food availability: females lactate at the time of leaf growth (young leaves have maximum protein content), and the young are weaned when a large surplus of food is available to all species.

DISCUSSION

The feeding strategies of the five nocturnal prosimian species inhabiting the dry deciduous forest of Marosalaza, near Morondava, can be illustrated by the average annual food intake or "dietogram." In Fig. 10, the dietograms proposed for the Malagasy species are only approximations, since the present study did not allow exhaustive measures of food intake. These estimates are compared to the results of Charles-Dominique (1977) concerning the diets of five other nocturnal prosimians (*Perodicticus potto, Euoticus elegantulus, Galago alleni, Galago demidovii,* and *Arctocebus calabarensis*) inhabiting the Gabon rain forest, where collection of stomach samples allowed more accurate measures of the quantity of the different food categories actually consumed.

Diets of the different species are related to the logarithm of the biomass (resulting in the definition of dietary grades, see above), because the carrying capacity of the environment depends on the overall production of leaves, fruits, and insects. Even in the two contrasting biotopes compared in Fig. 10, species of similar diet have a biomass of similar order of magnitude; for example, *Euoticus elegantulus* and *Phaner furcifer* both

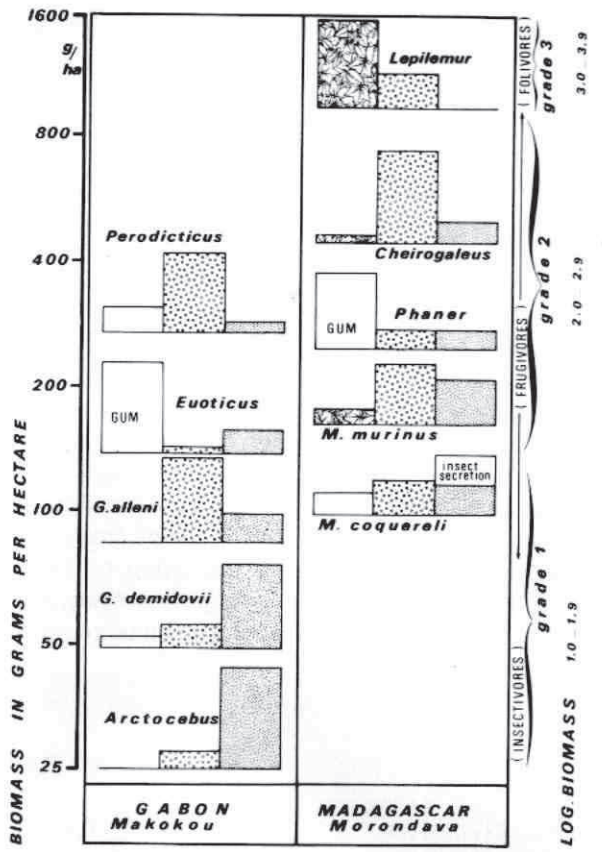

Fig. 10. A comparison of diets of the nocturnal prosimian species of Madagascar (Marosalaza forest) to those of the Gabon rain forest (after Charles-Dominique, 1977). Each species' diet is illustrated by the relative amount of leaves and/or gums (left rectangle), fruits (central rectangle), and animal matter (right rectangle) which have been ingested.

specialized on gum supplemented with invertebrate food (Chapter 3). Minor differences may result from the larger number of sympatric species inhabiting the rain forest, each of which has a more specialized diet and thus a more restricted quantity of potential food resources (Hladik and Chivers, 1978).

A characteristic pattern of food choices allows each species to be maintained in this complex and dynamic pyramid of producers and consumers. The mechanism allowing a certain flexibility together with a constant overall feeding tendency may involve different intensities in the respective effects of immediate hedonistic conditioning by taste stimulation, and long-term conditioning from food digestion and absorption (C. M. Hladik, 1978b). For instance, *Lepilemur ruficaudatus* is certainly mostly motivated by long-term conditioning after digestion of leaf material, whereas for *Microcebus* spp. the motivation to search actively for more nutritious fruits and insects may be related to a higher degree of taste stimulation and subsequent conditioning. In fact, this very crude analysis of feeding behavior does not seem sufficient to explain subtle differences nor constant overall tendencies in species such as *Phaner furcifer* and *Microcebus coquereli* which feed on many similar foods, but have nevertheless definite species preferences.

Seasonal Variations of the Dietary Tendencies

The dietary tendencies manifested by the different prosimian species present annual variations which have been qualified as preadaptations because, even in artifical conditions, the patterns of food choice vary according to the expected variations in food availability in the natural environment (Chapter 8). Such regular variations in feeding behavior may also exist in other species subject to regular and important annual changes of the environment. Nevertheless, the very marked variations in food availability and food consumption in the forest of the West Coast of Madagascar probably exert an intensive selective pressure which explains why the characteristic "seasonally variable feeding behavior" is firmly established in the five prosimian species thus far studied. However, the relative contributions of genetic inheritance and experience in the development of these patterns cannot yet be ascertained.

Further behavioral characteristics related to utilization of space and time reduce interspecific competition among the nocturnal prosimians of the Marosalaza forest by completing the overall differences in feeding behavior.

Utilization of Different Heights for Foraging

The different patterns of foraging described in this paper are illustrated in Fig. 11 by the mean heights and mean diameter of the supports on which the prosimians have been observed in the forest. Significant differences were determined by the t test applied to all possible pairs of species (calculation of t according to the means and standard deviations as in Chapter 8).

The differences in height are not significant for the species which have a feeding strategy sufficiently different to avoid competition; for instance, *C. medius* and *M. coquereli* ($p > 0.1$) which feed simultaneously only during the period of maximum (or surplus) food availability. In contrast, highly

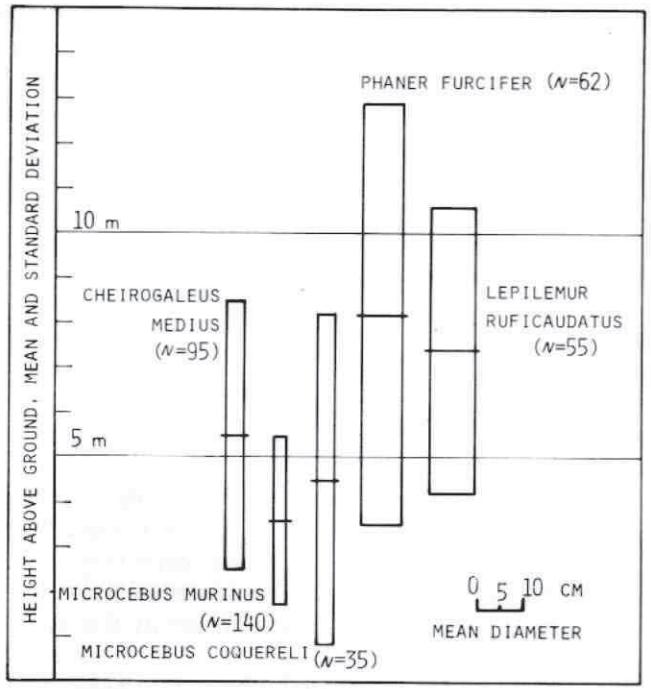

Fig. 11. Field location of the different nocturnal prosimian species in the Marosalaza forest. The height above ground where the animals were first observed are compared within species, and the thickness of each column is proportional to the diameter of the support used by the animals (after cumulative data of P. Charles-Dominique and C. M. Hladik).

significant differences ($p<0.001$) were found between *M. coquereli* and *Phaner furcifer* which are likely to compete for invertebrate food during the dry season, and between *C. medius* and *M. murinus* which have very similar food choices and similar yearly cycles.

The utilization of supports of different diameter merely reflects forest structure, with a significant difference ($p<0.01$) between *M. coquereli* and *P. furcifer* which also feed at very different heights.

Circadian Rhythms Considered in Terms of Food Niche Separation

The definite patterns of overall and feeding activity found by Pages and Petter-Rousseaux (Chapter 7) in the five species of nocturnal prosimians, also appear to be complementary to other distinctive adaptations reducing food competition.

The differential distribution of locomotor and feeding activity throughout the night tend to separate *C. medius* (mainly feeding at the end of the night) and the two *Microcebus* species (maximum activity at the beginning of the night, at least during periods of low food availability). By contrast, in *Phaner furcifer* the occurrence of gum feeding at the beginning of the night appears to be related mainly to intraspecific competition since individuals share (to a certain extent) the same trees producing gums (Chapter 3).

Although most cases of niche separation due to utilization of food resources at different times are best documented for nocturnal versus diurnal species (Charles-Dominique, 1975), intermediate cases were observed between diurnal primate species with different activity rhythms for feeding (Hladik and Chivers, 1978). The present study suggests that circadian rhythms of nocturnal species may also constitute an important component of the feeding strategy.

Finally, in the nocturnal world where the different prosimians apparently have very similar visual efficiencies (Chapter 5), the visual learning capacities may be important for developing different feeding strategies, since interspecies differences exist in the utilization of the "integrated" visual information, reflected by variations in transfer of learning, memory, and forgetting (Chapter 10). Thus sensory processes involved in the search for food sources must be considered as part of the overall species strategy.

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Summaries of Chapters

1. The climate of the West coast of Madagascar is characterized by a 7- to 8-month dry season. In the closed deciduous forest adapted to these conditions, about 200 woody plant species have been collected among which evergreen trees and lianas are present in limited number. Leafing times have been determined from the analysis of litter fall completed by records of herbarium specimens. A classification of leafing patterns is proposed, and flowering and fruiting patterns are briefly described. The seasonal variations of potential foods available to prosimians can be estimated from these data. The possible importance of toxic compounds has also been considered according to the results of a screening survey of alkaloids in leaves. The percentage of plants likely to be toxic (15%) has the same order of magnitude as in other tropical forests, but positive results appear more frequently among the evergreen species which are subject to folivore pressure during the dry season.

2. Annual variations in food production and composition in the forest of the west coast of Madagascar are presented in relation to different feeding strategies of five sympatric species of nocturnal prosimians. These strategies involve combination of physiological and behavioral characteristics which have been analyzed in the laboratory, and are presented in separate chapters in this volume. The results of laboratory tests are interpreted according to comparative results of the field studies. In *Cheirogaleus medius* and, to a lesser extent, in *Microcebus murinus,* the annual cycle of activity and lethargy plays a major role in the adaptation to variations in food availability. Nevertheless, seasonal variations in the patterns of food choices are a necessary complement to cope with overall changes in composition of the forest resources. In *Microcebus coquereli* and *Phaner furcifer,* behavioral specializations on insect secretions and plant exudates, which are the basis of their respective diets, are also complemented by additional cycles involving physiological variations. The most folivorous species, *Lepilemur ruficaudatus,* is also subject to variations in physiological/behavioral patterns, following the environmental changes in climate and plant production.

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